Neural Representations of Kinship

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Abstract:

While the fundamental relevance of kinship behavior for evolutionary and behavioral biology has long been recognized, the examination of kinship behavior from a neuroscience perspective is still in its infancy. Kinship is highly conserved from single-celled organisms to humans, where kin preferences are prevalent in behavior and language. Kin recognition is varied; with evidence for both genetic and both pre- as well as post-natal learning-based mechanisms. Learned kinship mechanisms are predominant in vertebrates and allow for flexibility regarding the concept of kin. We review new evidence for the lateral septum and its role in kinship behavior. We further discuss the discovery of *nepotopy*, a topographical representation of kin- and non-kin responsive neurons in the lateral septum. Neural representations of self/other, familiar/unfamiliar and kin/non-kin may support a circuit-level framework for a social template through which the mammalian brain learns, categorizes, and selects behavior based on perceived identity.

Highlights:

- Kinship behavior and kin recognition mechanisms are prevalent and multifaceted throughout most species.
- New evidence from behavioral, lesion and a topographic organization of kin-responsive neurons (*nepotopy*) supports a role for the lateral septum in mammalian kinship behavior.
- We propose that neural representations of kin/non-kin, self/other and familiar/unfamiliar individuals may support a theory of learned template/phenotype matching in kin recognition and social categorization.

Kinship behavior and kin recognition mechanisms in the natural world: prevalence and diversity

Individual recognition and categorization of identities is a challenge for biological systems that pre-dates the nervous system and continues to pervade all taxa of living organisms. Kin selection theory, proposed by Hamilton [1,2] has influenced evolutionary biology and behavioral science for more than 57 years now. Examples of kinship behavior in nature are sundry and the underlying biological mechanisms appear just as varied and complex [3]. Grossberg and Quinn while working at the Marine Biological Laboratory in Woods Hole, discovered an elegant form of kinship in single-celled larval colonies of the marine invertebrate *Botryllus schlosseri*. The pair identified unique genetic markers amongst larval colonies and produced a prolifera of F1 sibling larvae. Under two docks in Eel pond, they planted colonies consisting of siblings and consisting of unrelated larvae. The result they found after 4-weeks was that the sibling colony formed aggregates and the unrelated plot was widely dispersed. They further went on to show that mechanistically, kin recognition occurred through histocompatibility alleles at a locus known to regulate fusion. The fusion ability amongst siblings, it became apparent, was compatible with survival, reproduction, and resistance to parasitic loss (**Figure 1A**) [4].

Such elegant and thorough demonstrations of kinship from recognition to survival behavior are few and far between. Although preferential behaviors amongst relatives are readily seen upon examination, recent efforts to characterize kinship behaviors in filamentous fungi, beluga whales and bats reveal that the rules governing kinship behaviors are disparate and varied. Social behaviors in bats are not primarily predicted by kinship, though roosting behaviors were not [5]. Whale groups formed according to paternal lineage as opposed to the more often observed female-biased kinship organizations [6] and males travelling groups were mixed [7]. The world of kinship for fungal species is contentious and dramatic, where self/non-self recognition (allorecognition) mechanisms may exist in varied forms, contributing to ‘harming’, ‘helping’ and

‘cheating’ phenotypes where molecular pathways for each seem to have evolved for their own specialized form of self- and kin- preservation [8]. Another classic example for kinship behavior comes from peacocks in which recognition is proposed to arise from genetic mechanisms as pre-hatched peacock kin that are separated from one-another prior to hatching are seen to lek (i.e. engage in communal courtship) with one another despite a lack of post-hatch association (**Figure 1B**) [9].

Thinking of the adaptive value for kin recognition may provide insight into why kinship behavior is so highly conserved and at times specialized across species. E.O. Wilson loosely proposed 10 functional scenarios which are intertwined with kinship behavior: altruism towards siblings, parent-offspring interactions, allo-parenting, adoption, optimal outbreeding, schooling and aggregations, grooming, alarm signaling, avoidance of cannibalism and habitat selection [10]. An updated short (but not exhaustive list) of social behaviors which depend on kin recognition and are associated with positive/negative kin discrimination include: affiliation (e.g., pairbonds, coalitions), cooperation (e.g., for breeding/allo-parenting; acquisition and defense of resources; predator avoidance), parental care, filial/sexual imprinting, collective behavior (e.g., schooling, flocking), dispersal (which might facilitate proper habitat selection, avoidance of inbreeding- often sex-dependent). Nepotism (i.e. preferential treatment of relatives) is additionally a prevalent form of kinship affiliative behavior seen in everyday life; instances of nepotism in human beings have existed throughout history. An excellent example comes from a recent analysis of genome-wide mapping with anthropological and archaeological data regarding wealth found in gravesites of Bronze-age southern Germany. It was revealed that high-status kin groups and low-status non-kin divisions were formed and maintained over 700 years of analysis (**Figure 1C**) [*11]. A beautiful treatment of the role of kinship in the origins of human political organization is given in Fukuyama [12]. To this day, examples of human favoritism for kin are readily seen in politics, business and everyday life.

An unexpected, but remarkable indication that kinship might be a special category to humans comes from linguistics [**13]. In a recent large-scale cross-linguistic analysis, Thompson and colleagues observed that kinship terms show very strong semantic alignment across languages (**Figure 1D**). Despite the fact that kinship terms refer to abstract relations, their sematic alignment across languages eclipses that of many other natural categories that refer to concrete content (such as body or animal terms). Interestingly, even though kinship terms (along with expressions of quantity) are amongst the most translatable expressions across languages, human translators do not seem to be aware of this fact and do not rate kinship expressions as highly translatable in subjective judgements of translatability. Thompson and colleagues speculate whether the semantic alignment of kinship terms may be related to the organization of this terminology along few tight dimensions such as gender and generation. We suggest that kinship terms reflect evolutionary and deeply engrained 'natural' categories of the human mind.

Theories regarding the biological mechanisms of kin recognition are often categorized into several themes, including spatial distribution, association, phenotype matching and recognition alleles. Support for each mechanism can be found by looking into nature, with often several overlapping explanations. One recognition model may support a limited developmental period which may then transition based on sensory development or environmental changes. The cliff-dwelling bank swallow (*Riparia riparia*), for example, will parent a nest of mixed (kin and non-kin) fledglings based on proximity for a period until development of a signature call by chicks (around 15 days) allows sensory separation of offspring from foreign, then the parents will preferentially feed their genetic offspring selectively and reject unrelated chicks [14–16]. Thus, development often influences the nature of recognition and attribution to a single mechanism is rarely straightforward or possible.

Tags and learning in kinship: do learned mechanisms support flexibility of behavior and the concept of kin?

Of the proposed mechanisms for kin recognition, we will primarily discuss two broad possibilities: genetically derived 'tags' and learned kinship mechanisms (i.e. filial/sexual imprinting [17]). We suggest that evidence exists for both mechanisms and explore the possibility that learned phenotype matching mechanisms of kin recognition may have become highly specialized in vertebrates to support flexibility regarding the concept of kin.

As mentioned earlier, discrete genetically determined components/tags have been shown to be sufficient for kinship behaviors in invertebrates as was the case for Grossberg and Quinn's demonstration of kin-selective clustering by *Botryllus schlosseri*. They found that kin-selective clustering could be explained by shared alleles at a histocompatibility locus known to regulate fusion between adult colonies [4]. A more recent demonstration comes from a study of predatory nematodes *Pristionchus pacificus* which use allo-recognition mechanisms to distinguish their own kin from foreign offspring and cannibalize competing (non-kin) larvae. Lightfoot, Wilecki and colleagues discovered that the small peptide SELF-1 expressed on the nematode surface serves as the self-recognition signal in this case, allowing for kin recognition, which regulates non-kin cannibalization. They further showed that single-amino acid substitutions in SELF-1 can eliminate self-recognition (**Figure 2A**) [**18]. Non-kin directed, or heterocannibalism is seen in a plethora of species including gulls, spadefoot toads [19], sticklebacks, fruit flies (*Drosophila melanogaster*) [20] and sociological analysis of cannibalistic homicide indicates that non-kin killing may also extend to humans [21]. Comparative evolutionary analysis of heterocannibalistic species might reveal whether conserved genetic domains such as SELF-1 might contribute to a universal tag recognition mechanism for kin recognition related cannibalism or if recognition prior to heterocannibilistic behavior may also be learned in some instances.

Learned mechanisms of kin recognition (filial/sexual imprinting), supporting a category of phenotype matching, are remarkably diverse and prevalent in vertebrate species, thus presenting an attractive and tractable topic that neuroscience may be ready to tackle. Phenotype matching involves identification (and in some instances, learning/imprinting) of the characteristics of self or closely related kin and using these traits as a template on which recognition is judged. In phenotypic matching an observer makes the judgement regarding a subject and referential beings are those on which the kin template is based. The reference, or kin template might be the self or related kin [10,16,22] and/or the template might be learned through familiarity and exposure. The difficulty of a phenotype matching problem is not an easy task for biology to solve, thus further emphasizing the adaptive value required to produce such specializations. Engineers have tried replicating kin recognition of faces based on purely visual cues using computer vision, however the task has proven to be difficult [23, 24]. We propose that there is much to learn from looking into how biological systems have solved the problem. Kin recognition mechanisms may be multisensory, where animals may rely on olfactory, vocal/auditory, or visual cues to distinguish kinship [25–31]. Oftentimes, multiple sensory modalities are employed in one animal, such as in humans. Even when separated at the earliest stages after birth, newborns may select for playback of their mother's vocalization rather than the vocalization of another female [32]. Selective responses to the mother's odor are seen as early as 3–6 days after birth [33, 34, 22] and visual recognition of the mother opposed to strangers appears to occur later in development, though measures of this rely on detecting the behavioral response of the infant [35]. Rats also show preference for their own mother's amniotic fluid after birth compared to that of another mother [36] and when fetally exposed to apple scent, rats may prefer to drink fluids with the same scent after birth [37]. In mice, the onset of the first suckling episode is cued by maternal odor that is learned either in utero or immediately after birth [38]. These and other clues suggest that learning of kinship in the fetus can occur readily and across many species (**Figure 2B**).

In addition to pre-natal learned mechanisms, substantial evidence exists for a secondary window for kin-sensory learning (imprinting) post-natally. Numerous studies have confirmed postnatal learning mechanisms including a recent study of strawberry poisonous frogs (*Oophaga pumilio*), where it was shown that cross-fostering of frogs could lead to sexual preferences and male aggressive preferences selected for their learned, cross-fostered kin (**Figure 2C**). Furthermore, the authors showed evidence for these behaviors in speciation [*39]. In mice, recent evidence in wild species showed that cross-fostering could lead to behavioral preferences later in life [*40]. In rats, cross-fostered rats learn to prefer their cross-fostered siblings over strangers [41]. Learned/imprinted mechanisms for social behavior appear to be highly conserved and have been shown in goats/sheep [42], for learned vocal communication across colonies of naked mole rats [43] and sociological analysis of mate selection following co-rearing points to filial/sexual imprinting in humans as well [44, 45]. This, by no means exhaustive list of post-natal learning mechanisms, suggests that learned mechanisms may indeed be important in establishing neural circuits responsible for kin-directed behaviors. Furthermore, this brings forth the question of whether kinship itself might be a learned phenomenon that can be established with exposure and familiarity. Indeed, one would not question the fact that friends can become like family. Whether neural circuits for learned forms of kinship overlap with those for purely genetic relatives, is an open question.

Neurobiology of kinship: The lateral septum, '*nepotopy'* and 'social template theory'

While exemplars of kinship behavior in nature are widespread, we previously understood little about the underlying neural mechanisms. In our recent study, we present evidence from behavioral, lesion and a topographic organization of kin-responsive neurons which supports a role for the lateral septum in mammalian kinship behavior [**46]. To begin to probe the neural circuits that might be involved in kinship behavior, we looked for a behavioral paradigm to assess kinship in rodents and came across the work of Peter Hepper [41]. Hepper characterized sibling

preferences in newborn rats to juvenile ages and found that rat pups preferred their siblings from birth, a preference that changed with development. Hepper went on to show that cross-fostered pups preferred their cross-fostered (non-genetic) siblings to strangers and that genetic siblings separated closely after birth maintained sibling preferences despite the lack of postnatal familiarity. We replicated these sibling preference behavior experiments using a modified experimental apparatus and found a similar developmental trajectory of sibling preferences (sibling preference from birth changed to non-sibling preference around 15 days of age). A first hint of the brain structures involved came from the work of Moll and colleagues who performed functional imaging of humans with verbal kin stimuli and found activity in the human septal area [47]. We tested the hypothesis that lateral septum might be involved in this behavior by performing aspiration lesions in young sibling-preferring pups and old non-sibling preferring pups. We found that lateral septal lesions, but not lesions of the cortex made sibling preference go to chance levels (**Figure 3A**). To assess the dynamics by which neurons in the lateral septum might support kin preferences, we performed in vivo whole-cell patch-clamp and juxta-cellular recordings while presenting sibling, non- sibling, mother and non-mother odors as well as sibling and non-sibling ultrasonic vocalizations. We found that neurons were responsive to call and odor stimuli of kin and non-kin animals. When we compared recordings from young pups with older pups, we found that the greatest proportion of kin-responsive neurons was in the youngest time point, which decreased with age. (**Figure 3B**). In Hepper's and our work on kinship in rats, we show a distinct transition in behavioral kin-preference (sibling preference followed by non-sibling preference) which aligns with the onset of sensory modalities including hearing and vision. This behavioral transition, we found, correlated with a reduction in kin-responsive neurons and an increase in ongoing activity in the lateral septum. Ongoing spontaneous activity in sensory cortices shows a similar increase in frequency that is aligned with eye opening [48], thus the observed shift in the lateral septal neurons might reflect a change in input from sensory areas. When we mapped the coordinates of cells which were responsive to kin odors, we discovered that responsive neurons

were organized according to kinship, where sibling and mother odor responsive neurons were located more ventral in the lateral septum and non-sibling and non-mother odor responsive neurons were located more dorsal in the lateral septum. We propose that this organization may support kin-selective behaviors, we named this topographic organization *nepotopy* (**Figure 3C**) [**46].

Phenotype matching (as defined earlier) involves identification (and in some instances, learning) of the characteristics of self or closely related kin and using these traits as a template on which recognition is judged. In phenotypic matching an observer makes the judgement regarding a subject and referential beings are those on which the kin template is based. The reference, or kin template might be the self or related kin [10,16, 22] and/or the template might be learned through familiarity and exposure. We propose that the topographic organization of kin odor responsive neurons, or *nepotopy*, may serve as part of a template on which individuals perform identification and the selection of behavior based on perceived identity of self/kin/learned-kin and other. Two recent studies resulting from electrophysiological recordings showed that there are distinct spatial representations for self and other locations in neurons of the hippocampus of rats and bats [*49–51]. Another neural mechanism that may contribute to the recognition of kin could be familiarity tuned social responses. Kin, by mere association, are often extremely familiar and neurophysiological evidence from primates indeed indicates specific neural mechanisms for the processing of familiar faces [52]. Interestingly, cortical responses preferring familiar faces were observed in the perirhinal and anterior temporal cortex, i.e. in cortical areas that feed heavily into hippocampal processing streams.

The existence of cognitive representations from which flexible behavior is performed has been discussed and is increasingly applied to abstract concepts including identities in social space [53, 54, *55]. It is possible that familiar/unfamiliar as well as self/non-self representations in the hippocampus and kin/non-kin in the lateral septum may interact to form a template for social

identities, groups, and categories. Further experiments will determine whether a social cognitive template could be attributable to one region of the brain (potentially *nepotopy* of the septum), arising from network input or if the social template is itself a distributed network. Structural features of the septal, hippocampal connectivity may begin to provide insight into this notion, as the lateral septum receives extensive input from the hippocampus, which for a large part, is spatially segregated in dorsal and ventral pathways [56]. Emerging evidence does suggest that dorsal- and ventral- differences may exist in encoding spatial identity [57,58]. How the dorsal ventral projection of the hippocampus to the lateral septum might contribute to the formation of a social-kin-template or *nepotopy*, remains to be seen.

Overall, we present the topic of kinship to the field of neuroscience as a biologically rich topic that will only become more interesting with further investigation of the mechanisms and diversity at play.

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Author Contributions

A.M.C. and M.B wrote the paper. A.M.C. created figures and illustrations.

Declaration of interest: none

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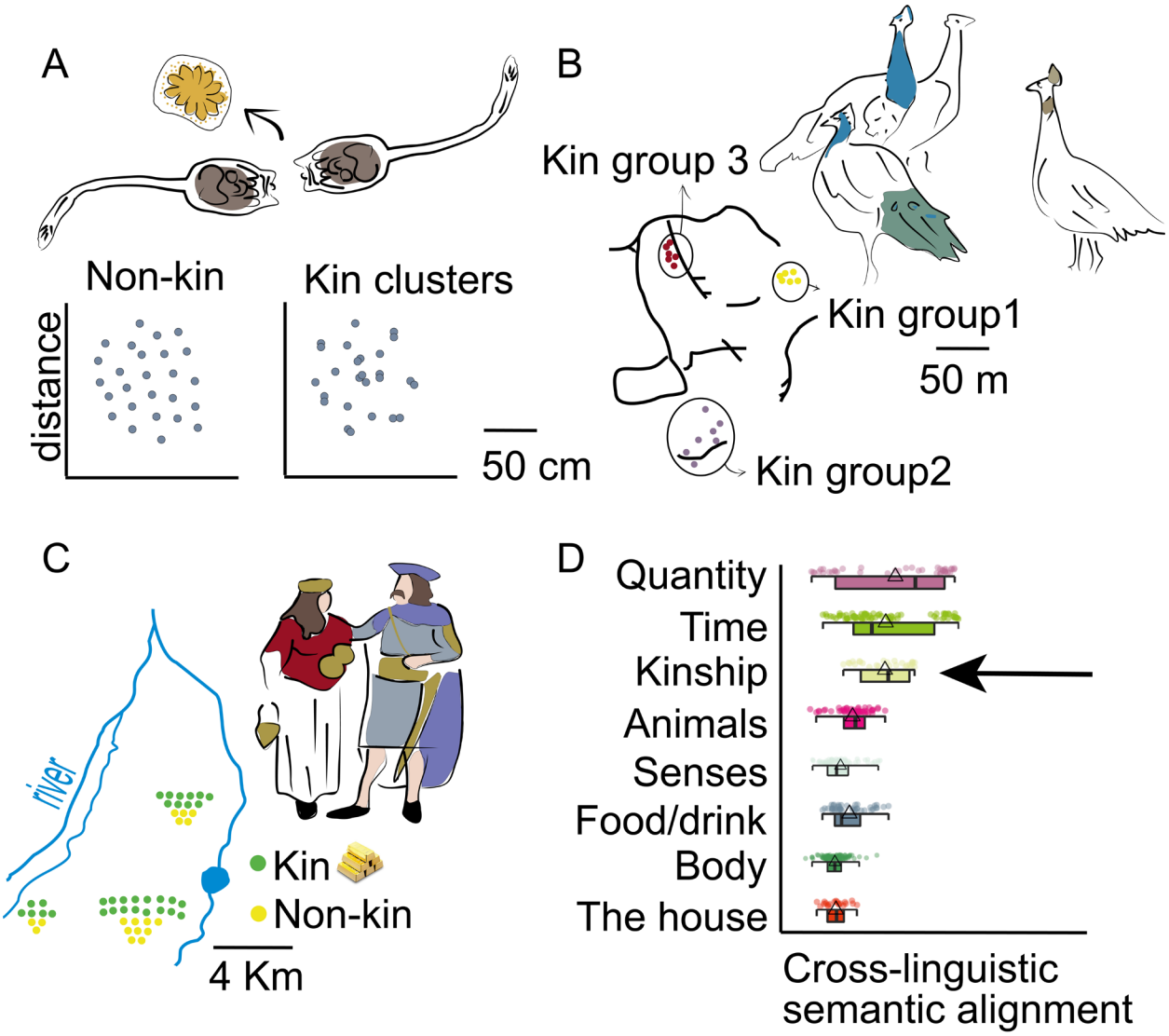

Figure 1. Kinship in animal, human behavior and language. A, The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate (Grosberg and Quinn 1986). B, Peacocks lek (i.e. engage in communal courtship) with relatives even in the absence of social and environmental cues (Petrie et al 1999). C, Kinship-based social inequality and nepotism in Bronze Age Germany (Mittnik et al 2019). D. Kinship terms (arrow) show remarkable cross-linguistic semantic alignment according to word embeddings (Thomson et al 2020). Such semantic alignment is astounding as kinship terms refer to abstract relations and their alignment eclipses that of many other natural categories that refer to concrete content.

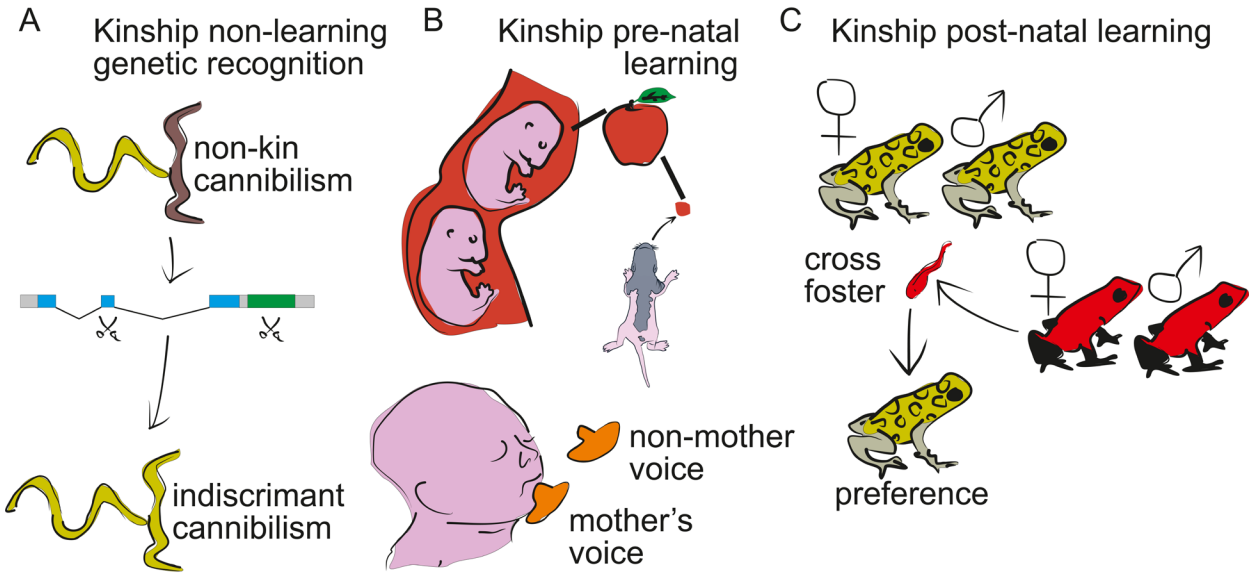

Figure 2. Kin-recognition mechanisms, learned and non-learned. A. An investigation of nematode cannibalism found that hetero-cannibalism of non-kin could be ablated with single nucleotide polymorphisms, suggesting non-learned mechanisms (Lightfoot et al 2019). B. In utero experiments with implanted odors along with postnatal learning suggest robust olfactory mechanisms are used by rodents to establish preferences after birth (Smotherman et al 1982). Human babies without post-natal exposure to the mother's voice show established preference to the maternal voice in a choice artificial nipple task which played-back the maternal voice opposed to a non-maternal voice (DeCasper et al 1980). C. Strawberry frogs that were cross-fostered showed altered mating and aggression preferences, suggesting post-natal learning mechanisms for kin-preferential behavior. The authors show that this behavior may drive speciation of frogs (Yang et al 2019).

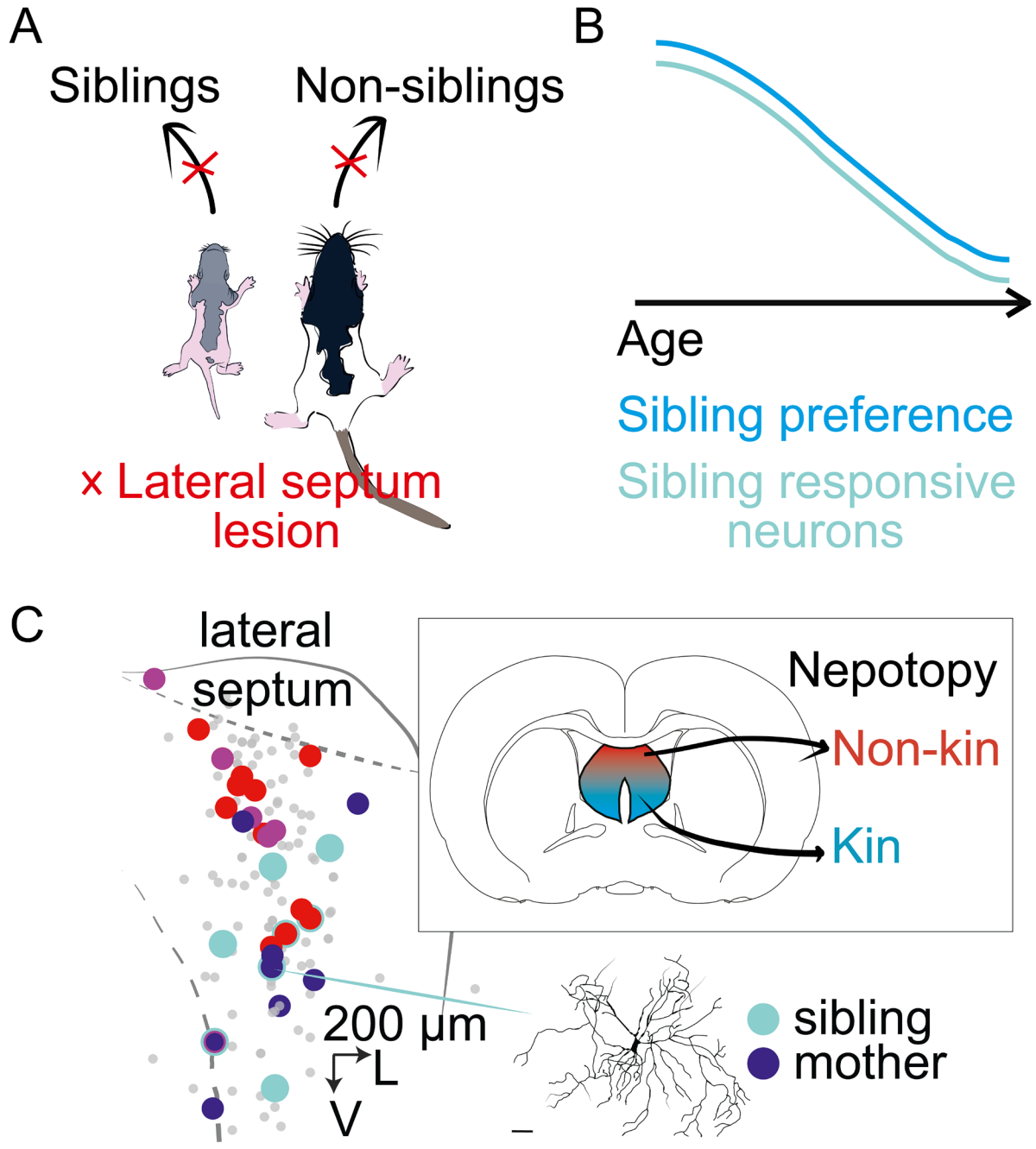

Figure 3: Neural basis of kinship behavior in the lateral septum. A. Sibling preferences in young pups and non-sibling preference in older pups were eliminated with lesions of the lateral septal region of the brain. B. Electrophysiological recordings showed that sibling odor preferring neurons were reduced with developmental age and ongoing activity was increased. C. Sibling-responsive cells were found to be located in a more ventral region of the lateral septum compared with non-sibling responsive neurons, a topography known as *nepotopy* (modified from Clemens et al 2020).